Distribution and Flight Behaviour of the Junglequeen Butterfly, *Stichophthalma louisa* (Lepidoptera: Nymphalidae), in an Indochinese Montane Rainforest

Vojtech Novotny, Martin Tonner and Karel Spitzer

Institute of Entomology, Czech Academy of Sciences, Branisovska 31, 370 05 Ceske Budejovice, Czech Republic

Abstract. A population of *Stichophthalma louisa* (Lepidoptera, Nymphalidae) was studied in a montane climax rain forest in Vietnam. The species was confined to the closed forest; open sites represented a barrier to its dispersal. The distribution within the forest was primarily determined by adult food sources (sap exuding from wounded trees of various species), which varied unpredictably in location and quality. As *S. louisa* tracked these resources, it was equally variable in its spatial distribution. Most of the variability in distribution was associated with feeding places and the network of gullies, "flyways" along which the butterflies flew. The turnover of individuals within any area (either a food place or the surrounding forest) was high. By the irregular and wide movements of individuals within the population, *S. louisa* is dissimilar to other tropical forest butterflies which have more predictable spatial structure of populations.

She came flying out of the wood over yonder — How fast those Queens can run! ... I'll make a memorandum about her, if you like — She's a dear good creature.

Lewis Carroll
Through the Looking Glass

Introduction

For pragmatic reasons most population studies on Lepidoptera have been on small populations of sedentary species confined to distinct and small "islands" of suitable habitat. Structurally simple and open temperate zone habitats, meadows in particular, are most frequently studied. In this study, the population structure of a forest butterfly *Stichophthalma louisa*, which is confined to a large area of a structurally complex montane monsoon forest, is examined.

Stichophthalma louisa Wood-Manson 1877 is a montane species with the distribution from Upper Burma, northern and central Thailand to North Vietnam. The isolated, little known and highly variable populations of northern Vietnam appear to form several local geographical races (Fruhstorfer, 1927). Most of specimens from the study site, the Tam Dao Mts., can be probably referred to *S. louisa sparta* de Niceville 1894 (Niceville, 1894; Okano, 1985; P. Ackery pers. com.), but typical "*louisa*" and intermediates are also present. The life history is unknown. Most

species of the genus *Stichophthalma* are probably univoltine with larvae associated with monocotyledonous plants (Fruhstorfer, 1927). According to Ackery (1988), larvae of a related Chinese species *S. howqua* Westw. feed on *Phyllostachys* spp. (Poaceae).

Methods

STUDY SITE

The study site was a large remnant of a montane rain forest (19,000 ha) in the Tam Dao Mts. (N. Vietnam; 21° 30' N, 105° 40' E; 800 - 1000 m alt). It is floristically very rich, without any conspicuously dominant tree species. The tree layer formed a dense continuous canopy, approximately 10 m high, without emergent trees, but with epiphytes and climbers (Figs. 1 and 2). Bamboo thickets dominated on ridge tops and disturbed sites, the shrub and ground layers were fragmented (Spitzer et al. 1993).

As steep slopes and dense vegetation made movement through the forest difficult, observations on the population of *S. louisa* were confined to a 5-meter wide belt on either side of a narrow path tracking a contour at 800 m asl. The path was only about 1 meter wide and did not affect the composition of the surrounding vegetation. It intersected an extremely steep slope (30° - 40°) so the canopies of the trees growing down-hill could be observed. A transect of 2 km was demarcated along this path, arbitrarily divided into 200 10-meters long sections numbered 1 - 200. The transect intersected three habitat types: closed forest (sections 1 - 112, 1120 meters), ecotone with forest on the down-slope and a deforested area on the up-slope (113 - 167, 550 meters), and ruderal (168 - 200, 330 meters). The ruderal zone was a mosaic of small cultivated fields and abandoned land overgrown by

Fig. 1 The Tam Dao mountains covered by rain forest.

tall grasses. Butterfly communities along the transect were described by Leps and Spitzer (1990) and Spitzer et al. (1993).

Along the forest transect, five habitat types were distinguished among the 112 forest sections: closed forest, gullies, bamboo thickets, glades, and feeding trees. Shallow rocky gullies with either permanent or temporary brooks were numerous within the forest. As the transect intersected the slope horizontally, the gullies were perpendicular to it. They represented "tunnels" within the vegetation, with closed canopy above. Dense bamboo thickets covered small-scale disturbed patches, usually the result of selective logging. Glades were open patches ranging from tens to hundreds of square meters, either rocky or overgrown by grasses. They were either of natural origin or from human disturbance. Feeding trees were trees which exude sap and that are used as the major nutrient resource by adult butterflies.

Our observations were made daily, between 10.00 and 18.00 hour, from 5 June to 7 July 1991. This was the first half of a rainy season (rainy season starts in June and ends in October).

BUTTERFLY DENSITY, DIURNAL ACTIVITY, AND MOVEMENTS

The number of *S. louisa* was estimated by direct counts of individuals flying or resting on the vegetation within the 10-meter wide belt along the forest transect (sections 1 - 112). Altogether, 65 transect counts were conducted. Our observations depended on butterfly activity recognizing that some of the resting, but none of the flying, individuals were overlooked. Accordingly only results under optimum weather conditions provided reliable density estimations.

The number of butterflies recorded flying per unit time during the forest transect counts was an index of activity used to evaluate diurnal activity of *S.*

Fig. 2 Montane monsoon forest in the Tam Dao Mts., the habitat of *Stichophthalma louisa*.

louisa. Altogether, data on 389 specimens recorded between 10.00 and 18.00 hour over 32 hours of observation were analysed.

Movement of *S. louisa* was examined by a capture-mark-recapture method between 8 June and 7 July 1991 (see Fig. 3). Because of the dense forest vegetation, butterflies were captured and marked only along the transect, which was effectively a one-dimensional linear structure across a two-dimensional population continuum, not permitting home range, population size and other demographic estimations.

Results

BUTTERFLY BEHAVIOUR

Stichophthalma louisa is cryptic, the upper and undersides of their wings resemble dead leaves. When resting on vegetation, butterflies close their wings. When flying, they slowly glide in a zigzag course within the vegetation, resembling falling leaves. Encounters between two butterflies frequently resulted in a "contest" during which the couple repeatedly spiralled upwards with the butterflies clinging together.

As other amathusiines, *S. louisa* was never seen visiting flowers. The only observed source of food for butterflies was sap bleeding from injured trees. When feeding, butterflies ignored one another, frequently sitting side by side in a vicinity of the sap flow.

SEASONALITY

The seasonal dynamics of the Tam Dao population can only be inferred from our short-term observations made at various times over several

Fig. 3 Marked specimen of *Stichophthalma louisa*.

years. This information indicates a distinct seasonality with the occurrence of adults restricted to the June to September rainy season, with the highest abundance during June - July. No adult butterflies were observed in May, October, and December. The present study coincides with the period of high butterfly abundance following peak emergence. Freshly emerged specimens were observed throughout the course of the study, but the proportion steadily decreased from 87 % at the very beginning (5 - 10 June) to 36 % between 23 and 28 June.

DIURNAL ACTIVITY

The activity varied widely from 5 to 34 butterflies observed per hour and did not reveal a consistent daily pattern. *S. louisa* was a typical diurnal species, not crepuscular like some other amathusiines. The periodicity observed on any given day possibly followed fluctuations in weather.

VERTICAL DISTRIBUTION

Stichophthalma louisa had a distinct vertical distribution, being confined mostly to the canopy and top of the shrub layer with a flight height range 2 - 8 m. The population density of *S. louisa* observed in the shrub understorey vegetation (0 - 2 m) close to the transect was approximately 1.4 butterflies per hectare. This value is ten times lower than that for the canopy (see below). *S. louisa* was never observed to fly above the canopy layer.

HABITAT PREFERENCE

The number of butterflies observed along the transect is summarized in Table 1. Altogether, 65 transect counts were made and each butterfly seen was assigned to its transect section. *S. louisa* appeared to be restricted to the forest, its edge represented a barrier that was rarely crossed. Glades within the forest habitat, although small, were avoided. Butterflies were also rarely encountered in patches of very dense vegetation, especially bamboo thickets. On the other hand, butterflies were observed flying more frequently along gullies and brooks than in the surrounding dense forest.

The proportion of the transect sections classified as a particular habitat type gives a rough idea of its representation within the forest (Table 1). Closed canopy forest covered about 77 % of the transect, 13 % was covered with bamboo thickets and the remaining 10 % were open glades. Along the 1120 m of the transect there were 15 gullies (spanning over 19 sections), five of which were bisected by a permanent brook. In the forest natural glades were scarce and small. Such glades were common along the transect due to man-made clearings. These together spanned over 10 transect sections. Naturally produced feeding trees had a density of about 1.2 per hectare, with two out of five feeding trees bleeding sap due to man-made injuries.

Of 812 butterflies recorded, 38 % were found within the closed forest, 25 % flying along gullies, and 29 % in sectors with a feeding tree. In terms of butterfly distribution, glades and bamboo thickets were not important as each of these habitats harboured less than 5 % of the population.

The variance/mean ratio for the closed forest, $s^2/\bar{x} = 2.1$, is fairly close to unity, although significantly different from it (x^2 test, $P>0.05$). This indicates that the distribution of *S. louisa* in the closed forest is close to random, not clumped (Poisson distribution has the variance/mean ratio equal to unity). Accordingly, no further differentiation of the closed forest habitat type into subhabitats is probably needed.

Dispersion of *S. louisa* within each habitat is expressed by the Lloyd's index of mean patchiness (Pielou, 1976) as given in Table 1. Distribution of butterflies among 19 gullies and brooks was highly heterogeneous. There were five sections used as flyways with densities ranging from 16 to 22 butterflies. Another 14 sections showed densities not different from the closed forest habitat (1 - 9 butterflies per section, mean 4.5). The occurrence through time of butterflies in the high-density sections was uneven and fluctuated independently in the various sections. This is shown in Fig. 4, which depicts the numbers of butterflies observed each day over one month sampling period across three adjacent flyways (sections 77, 74, 70).

Feeding trees differed in their attractiveness for *S. louisa*, indicated by a high value of Lloyd's index. The attractiveness of any given feeding tree

Table 1. Habitat and microhabitat preferences of *Stichophthalma louisa*.

Habitat	n	N	$\bar{x}$	s^2	
Forest	112	812	7.2 a	158.2	
Ecotone	55	31	0.6 b	1.1	
Ruderal	33	4	0.1 b	0.3	
Forest microhabitat	**n**	**N**	$\bar{x}$	s^2	**L**
Feeding trees	5	236	47.2 a	1279.7	1.6
Gullies and brooks	19	203	10.7 b	141.8	2.2
Closed forest	62	293	4.7 c	10.1	1.2
Bamboo thickets	14	34	2.4 d	2.6	1.0
Glades	12	28	2.3 d	4.4	1.4

All habitat types are characterized in the text. The forest habitat is further subdivided into 5 microhabitats in the lower part of the table. n = number of 10-meters section in the transect. Total number of butterflies recorded (N), arithmetic mean ($\bar{x}$), and variance (s^2) of butterfly numbers per section, and Lloyd's index of mean patchiness (L) are given for each habitat. Values in lines followed by the same letter are not significantly different ($P>0.05$; Kruskal-Wallis test).

as a food source varied over time. This variability was not correlated with changes in butterfly numbers on other feeding trees or in the surrounding forest and neighbouring gullies used as flyways (Spearman correlation coefficient between number of butterflies observed per day on a feeding tree and in surrounding forest were not significant, P>>0.05, for all feeding trees).

Stichophthalma louisa did not create large aggregations in any forest habitat type. On feeding trees, no more than 6 specimens were ever present simultaneously. No hilltopping or response to other obvious landmarks were observed, although all neighbouring prominent summits were inspected. The butterfly was never observed to indulge in puddling behaviour. At night, the butterflies roosted singly in the vegetation. During the 65 sampling periods of the forest transect sections, 8 specimens was the maximum recorded at any one time.

POPULATION DENSITY AND MOVEMENTS

The number of *S. louisa* counted during any transect sample ranged from 1 to 26 (mean 18.4). Since the transect represents an area of 11,200 sq. m. (1120 m × 10 m), the mean population density of *S. louisa* in the forest was 16.4 individuals per hectare. The observed density remained constant over the study period.

A total of 235 butterflies were marked and released, with 524 butterflies checked for marks from 8 June though 7 July. Only 23 previously marked butterflies were recaptured. The low recapture frequency indicates that butterfly mortality was high and/or they were very transient,

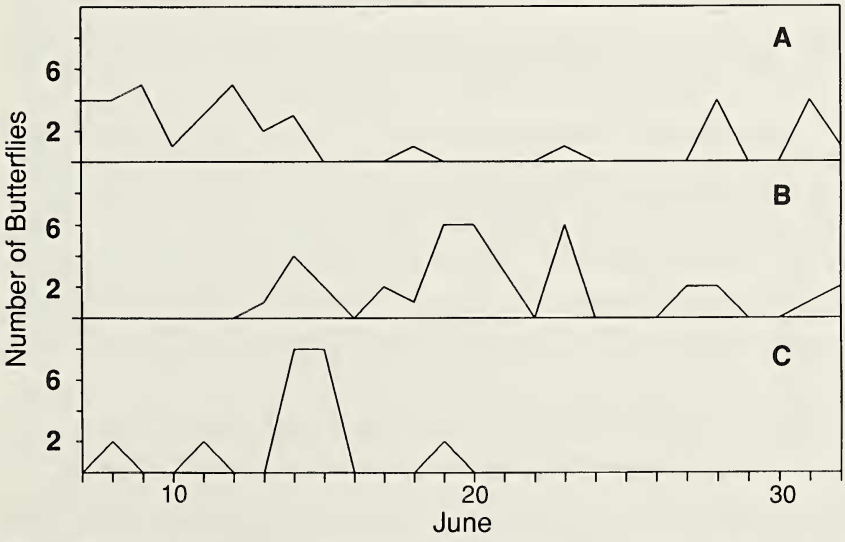

Fig. 4 The number of *Stichophthalma louisa* observed flying along gullies. No records were made on 16 and 22 June due to bad weather. A section 77, gully with a brook; B section 74, dry gully; C section 70, dry gully.

moving widely across the forest. The possibility that butterflies react to marking by leaving the study area cannot be discounted, but no such escape behaviour was observed in freshly marked butterflies. High mortality cannot alone be an explanation as a high percentage of specimens had worn wings and recaptured individuals showed a low decay rate. Our data do not permit discriminating between these processes.

Stichopthalma louisa is able to move over considerable distances in a short time. The average distance travelled by recaptured butterflies was 122 m, with the longest travelled in a single day of 460 m. Another butterfly was seen visiting two feeding trees 270 m apart during a 15 minute interval. The longest time elapsed between a capture and recapture of a butterfly was 17 days.

Thirty three butterflies were marked on the feeding tree in section 31, but none was recorded again among the total of 107 specimens observed at the section. Between 17 and 21 June, 39 butterflies were recorded on the feeding tree in section 7. They all were captured and marked. Among them, only one butterfly visited this tree repeatedly. This suggests a low frequency of repeated visits by a particular butterfly with a high turnover rate of individuals on particular feeding tree.

Discussion

The few tropical forest butterflies studied thus far have a rigid population structure with fixed home ranges and/or a predictable pattern of movements (*Heliconius* spp.: Gilbert & Singer, 1975; *Morpho* spp.: Young, 1971, and references therein). The data obtained in this study indicate that *S. louisa* individuals move widely and irregularly.

A general picture of movement of *S. louisa* within the study area emerges. The occurrence of butterflies was primarily determined by the availability of food sources, which were unpredictable and varied in location and quality. Consequently, the *S. louisa* population, which tracked these resources, was equally variable in its spatial distribution. Most of this variability was associated with the distribution of feeding places and the network of gullies along which flight paths of the butterflies were concentrated. In contrast, within the remaining area of the closed forest the dispersion of the population was fairly close to random and did not vary over time. The turnover of individuals within any area, either food sites or the forest, was high.

A wide spectrum of spatial patterns and flight behaviour has been reported in butterflies (e.g. Gilbert & Singer, 1975). The two principal factors that determine flight behaviour are the species' reaction to patches of unsuitable habitat and mobility of individuals within a suitable habitat. Areas of unsuitable habitat either do not represent barriers to movement so that any given population may be distributed across several "habitat islands" (e.g. *Erebia epipsodea*: Brussard & Ehrlich, 1970a, b, c), or else the unsuitable habitat may be barrier to the

dispersal of populations (e.g. *Heodes virgaureae*: Douwes, 1975; *Euphydryas editha*: Ehrlich, 1965; *Mellicta athalia*: Warren, 1987). Within a suitable habitat, individuals are restricted by their mobility to a particular area that may be either fixed or changing over time. A home range may be fixed by some recognition behavior (*Philotes sonorensis*: Keller et al., 1966), by use of a visual landmark as a meeting point for mating (*Oeneis chryxus*: Daily et al. 1991), as a site for gregarious nocturnal roosting (*Marpesia berania*: Benson & Emmel, 1973), or by a particular distribution of feeding sources which a butterfly exploits (*Heliconius ethilla*: Ehrlich & Gilbert, 1973).

Of butterflies studied so far, *S. louisa* belongs to those species in which the population is kept within an area by strict avoidance of unsuitable habitats, but individuals move widely and irregularly within favourable habitats. There were no constant features in the spatial pattern resembling the regular repeated flights of individuals along particular routes as in *Heliconius* spp. (Gilbert & Singer, 1975). Ehrlich & Gilbert (1973) speculate that the "scheduled" flights of *Heliconius* represent optimum foraging routes. Clearly, there are no feeding routes that are permanently optimum for *S. louisa* due to temporal variability in its primary food source. Because of this, the distribution patterns of *Heliconius* and *S. louisa* populations differed greatly although both were determined mainly by the pattern of adult food resources, a pattern found in other species of butterflies (e.g. Brakefield, 1982; Gilbert & Singer, 1973; Douwes, 1975).

Acknowledgements. This work was supported by the International Council for Bird Preservation and Flora & Fauna Preservation Society grant. We thank R. H. T. Mattoni, A. F. G. Dixon, J. Leps, P. R. Ackery, and an anonymous referee for their invaluable comments and advice on this manuscript.

Literature Cited

Ackery, P.R. 1988. Hostplants and classification: a review of nymphalid butterflies. Biological Journal of the Linnean Society 33:95-203.

Benson, W.W. & T.C. Emmel. 1973. Demography of gregariously roosting populations of the nymphaline butterfly *Marpesia berania* in Costa Rica. Ecology 54:326-335.

Brakefield, P.M. 1982. Ecological studies on the butterfly *Maniola jurtina* in Britain. I. Adult behaviour, microdistribution and dispersal. Journal of Animal Ecology 51:713-726.

Brussard, P.F. & P.R. Ehrlich. 1970a. The population structure of *Erebia epipsodea* (Lepidoptera: Satyrinae). Ecology 51:119-129.

——. 1970b. Contrasting population biology of two species of butterfly. Nature 227:91-92.

——. 1970c. Adult behavior and poulation structure in *Erebia epipsodea* (Lepidoptera: Satyrinae). Ecology 51:880-885.

Daily, G.C., P.R. Ehrlich & D. Wheye. 1991. Determinants of spatial distribution in a population of the subalpine butterfly *Oeneis chryxus*. Oecologia 88:587-596.

Douwes, P. 1975. Distribution of a population of the butterfly *Heodes virgaureae*. Oikos 26:332-340.

Ehrlich, P.R. 1965. The population biology of the butterfly, *Euphydryas editha*. II. The structure of the Jasper Ridge colony. Evolution 19:327-336.

Ehrlich, P.R. & L.E. Gilbert. 1973. Population structure and dynamics of the tropical butterfly *Heliconius ethilla*. Biotropica 5:69-82.

Fruhstorfer, H. 1927. Amathusiidae. In: A. Seitz (ed.): Die indo-australischen Tagfalter - Die Grossschmetterlinge der Erde. Bd. 9. A. Kernen, Stutgart, pp 403-452. butterfly species. American Naturalist 107:58-72.

Gilbert, L.E. & M.C. Singer. 1973. Dispersal and gene flow in a butterfly species. American Naturalist 107: 58-72.

——. 1975. Butterfly ecology. Annual Review of Ecology and Systematics 6:365-397.

Keller, E.C., R.H.T. Mattoni & M.S.B. Sieger. 1966. Preferential return of artificially displaced butterflies. Animal Behavior 14:197-200.

Leps, J. & K. Spitzer. 1990. Ecological determinants of butterfly communities (Lepidoptera, Papilionoidea) in the Tam Dao Mountains, Vietnam. Acta Entomologica Bohemoslovaca, 87:182-194.

Niceville, de L. 1894. New or little-known butterflies from the Indo-Malayan Region. Journal of the Asiatic Society of Bengal 63:1-59.

Okano, K. 1985. Descriptions of four new butterflies on Amathusiidae Nymphalidae and Papilionidae (Lepidoptera). Tokurana 10:1-17.

Pielou, E.C. 1976. Mathematical Ecology. Wiley & Sons, New York.

Spitzer, K., V. Novotny, M. Tonner & J. Leps. 1993. Habitat preferences, distribution and seasonality of butterflies (Lepidoptera, Papilionoidea) in a montane monsoon forest. Journal of Biogeography, 20: xxx [in press]

Warren, M.S. 1987. The ecology and conservation of the heath fritillary butterfly, *Mellicta athalia*. II. Adult population structure and mobility. Journal of Applied Ecology 24:483-498.

Young, A.M. 1971. Wing coloration and reflectance in *Morpho* butterflies as related to reproductive behavior and escape from avian predators. Oecologia 7:209-222.